HOW AN INCREASED EFFORT TO KILL WOLVES
WOULD BENEFIT CARIBOU POPULATIONS
IN THE NORTHWEST TERRITORIES

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ABSTRACT

Wolves are the most important predator on barren-ground caribou. This paper reviews the theoretical and practical reasons why an increased effort to kill wolves would benefit caribou populations. Theory suggests that wolves may regulate caribou members and are more likely to do so at low caribou densities and when caribou are hunted. All adequately monitored wolf removal experiments have been followed by increases in caribou numbers. Regardless of how many wolves were killed, we predict that an increased effort to kill wolves would benefit Northwest Territories caribou herds.

INTRODUCTION

Wolves (<u>Canis lupus</u>) are the most important predator of caribou and are found on all barren-ground caribou (<u>Rangifer tarandus groenlandicus</u>) ranges in the Northwest Territories (NWT) except Coats Island (Heard 1982). The NWT Wildlife Service and the Caribou Management Board[1] is considering management options that will increase the size of the Kaminuriak (Simmons et al. 1979) and Beverly (Heard and Decker 1980, Gunn and Decker 1982) herds and produce population increases. Increasing the wolf kill is one such option.

Wolves have a major influence on caribou population dynamics but the effect of an increased effort to kill wolves on caribou population size depends on; 1) how wolf numbers would be affected, 2) how wolf numbers affect caribou numbers, and 3) compensatory changes if any, in other mortality factors.

This paper addresses those three questions by, discussing; 1) theoretical predator prey relationships, 2) the relationship between field studies and predator-prey theory, and 3) our predictions of how an increased effort to kill wolves would benefit NWT caribou populations.

This report is designed to assist decision makers. It is based primarily on a review of the literature and also draws from the expertise of wildlife managers in British Columbia and Alaska and from biologists at the University of British Columbia.

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[1] The Caribou Management Board is composed of public and government representatives empowered to recommend appropriate management actions concerning the Beverly and Kaminuriak caribou herds to politicians. The NWT Wildlife Service has the sole responsibility for recommending management action on other herds.

PREDATOR PREY THEORY

Logistic population growth (Fig. 1) can be represented by a dome-shaped net reproduction curve (Fig. 2). Net reproduction expressed as a percent of population size (Fig. 3) declines linearly with increasing population size and is determined by the combined effects of birth and death rates. These curves (Figs. 1, 2 and 3) are probably useful models of caribou populations. Because caribou birth rates show little variation (Dauphine 1976, Bergerud 1980, Don Thomas, Can. Wildl. Serv. pers. comm.) the percent net reproduction curve can be considered to be solely a function of changes in mortality.

The shape of the mortality curve (mortality vs. density) represents the combined effects of all causes of death, of which we will consider three; intra-specific competition for food, wolf predation and hunting. 1) If intra-specific competition for food were the only cause of mortality in a population we would expect it to be density - dependent, regulating the population as shown in Figure 3. 2) The possible shapes of a mortality curve representing predation losses was determined by Holling (1959). He demonstrated that predators can respond to changing prey densities in two ways: functionally and numerically. Functional responses refer to the ability of predators to capture and consume their prey at different prey densities. The numerical response refers to the predator's ability to convert prey into more predators. The functional response curve shows saturation at high prey densities because predators have a minimum handling time per prey. The numerical response curve also asymptotes because, like

$$N = \frac{K}{1+e^{a-rt}}$$

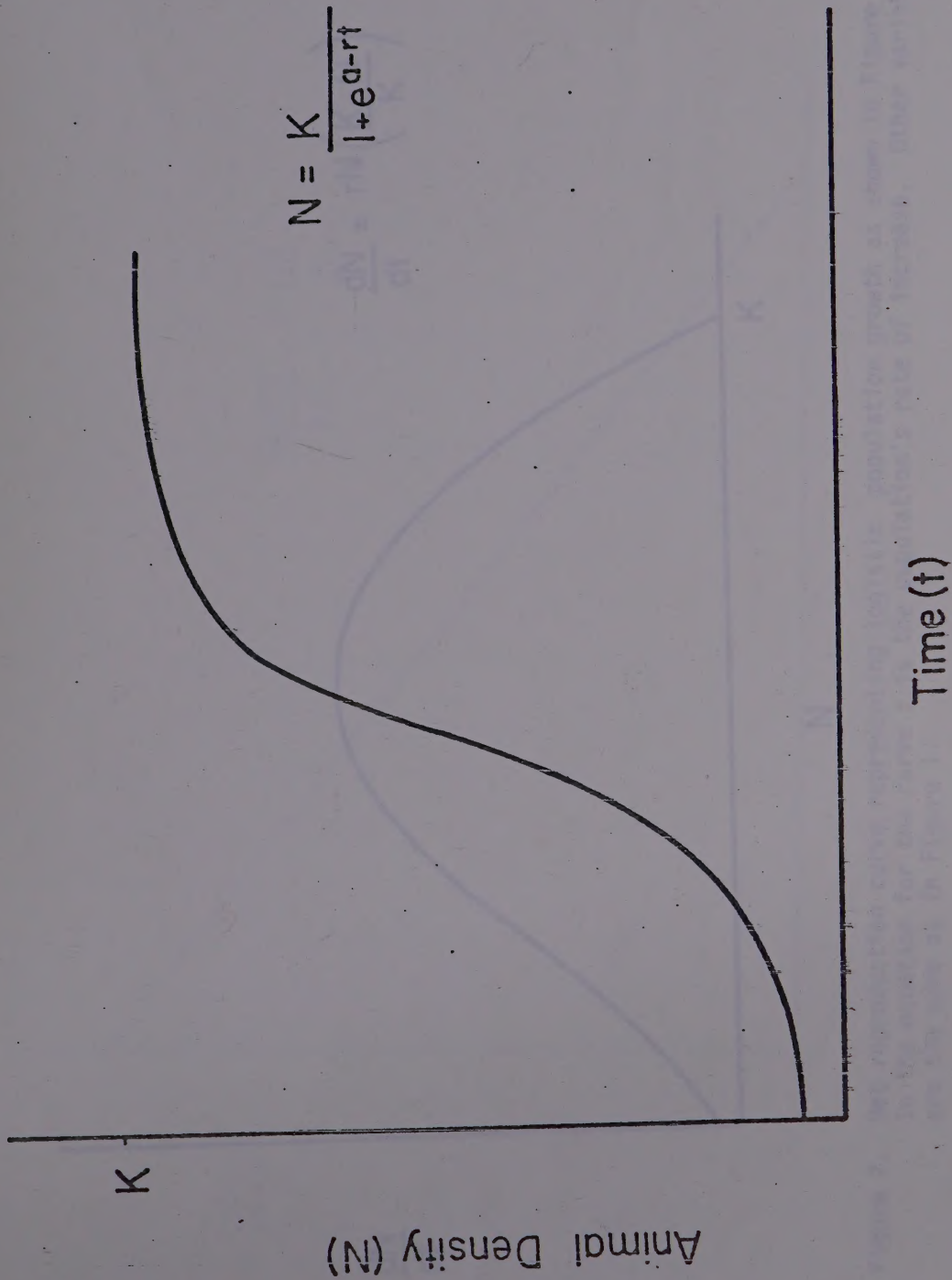**Time (t)**

Animal Density (N)

K

Figure 1. Logistic population growth curve and the equation for the curve. K is the maximum population density (N), a is a constant of integration defining the position of the curve and e is 2.71828, the base of natural logarithms.
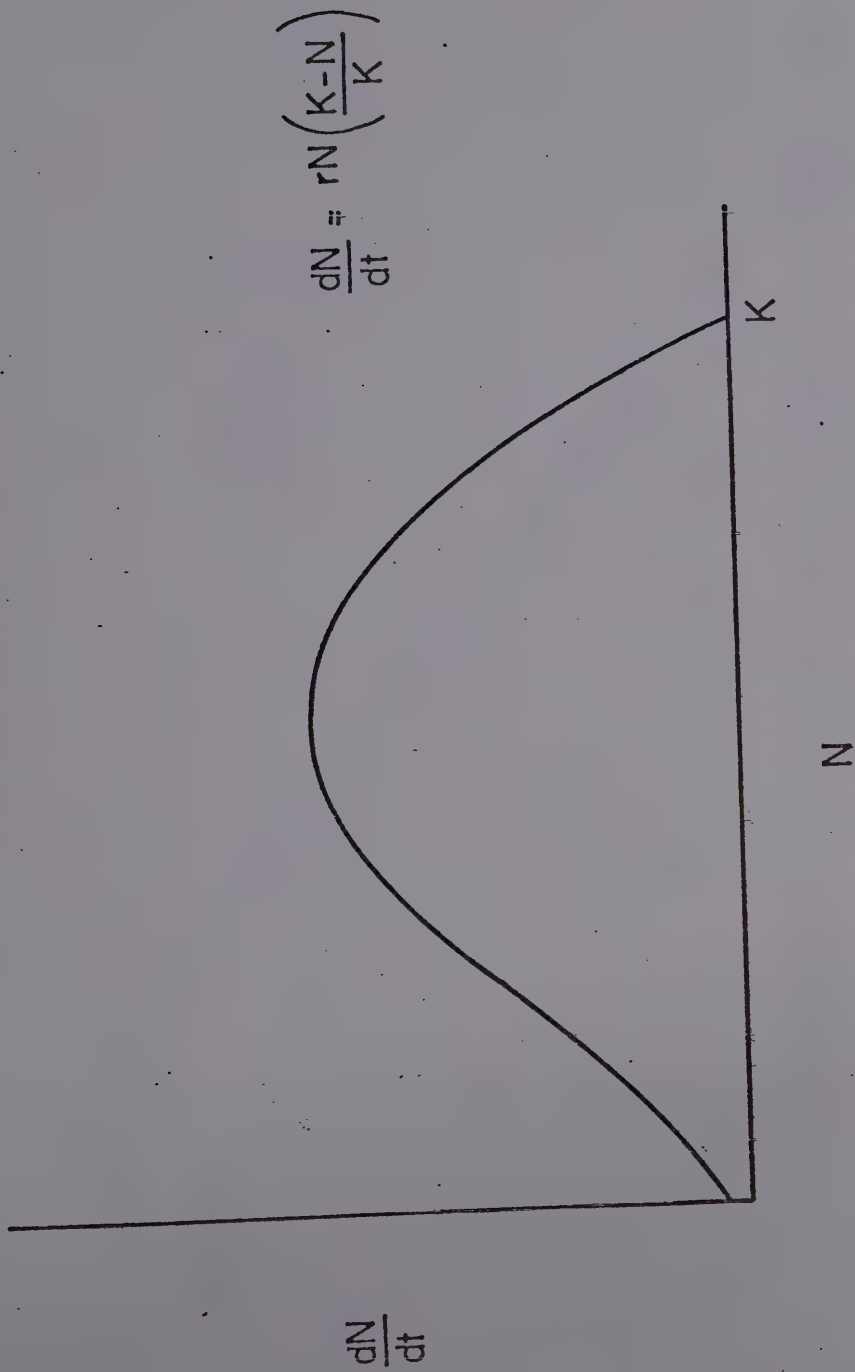
$$\frac{dN}{dt} = rN\left(\frac{K-N}{K}\right)$$

Figure 2. Net reproduction curve representing logistic population growth as shown in Figure 1. In the equation for the curve r is the population's rate of increase. Other variables are the same as in Figure 1.
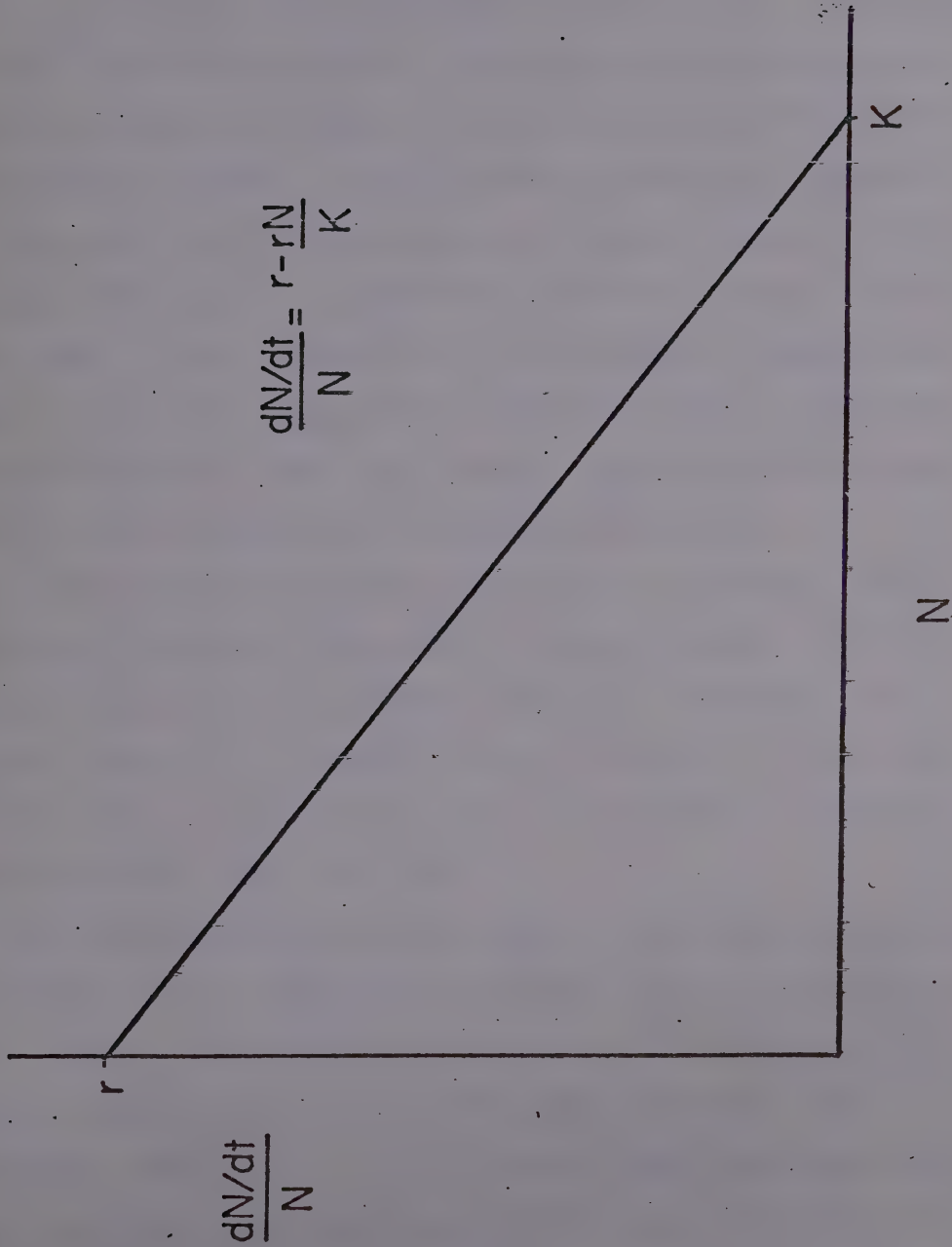
Figure 3. Net reproduction curve representing logistic population growth where net reproduction is expressed as a percent of population density. All variables are the same as in Figure 1 and 2.

$$\frac{dN/dt}{N} = r - \frac{rN}{K}$$

all populations, predators cannot continue to increase indefinitely.

Functional and numerical response curves are linked to produce a combined predation mortality response curve indicating the proportion of prey eaten at varying prey densities (Fig. 4). At low prey densities predators take a greater proportion of prey as prey numbers increase. Beyond a certain density the proportion taken decreases with increasing prey density because of the saturation behaviour of the functional numerical response curves. The key point is that if predation is high enough to regulate prey numbers it may do so only over a restricted range of relatively low prey densities. Once prey numbers move beyond that range, predators have less influence on prey population sizes.

3) The functional response of hunters is unknown. Hunting pressure may be largely independent of caribou density, depending perhaps on economic or cultural factors. Hunters show no numerical response to changing caribou densities. The hunting mortality curve is therefore probably a much flattened version of the wolf mortality curve (Fig. 4).

The combined mortality curve cannot be determined simply by the addition of the competition, predation and hunting mortality values unless those mortality agents are noncompensatory. Errington (1956) championed the idea that predation acted in a compensatory fashion. By this he meant that predators killed animals that would otherwise have died from some other cause. The distinction between compensatory and noncompensatory mortality is probably a matter of degree, not a choice between two alterna-
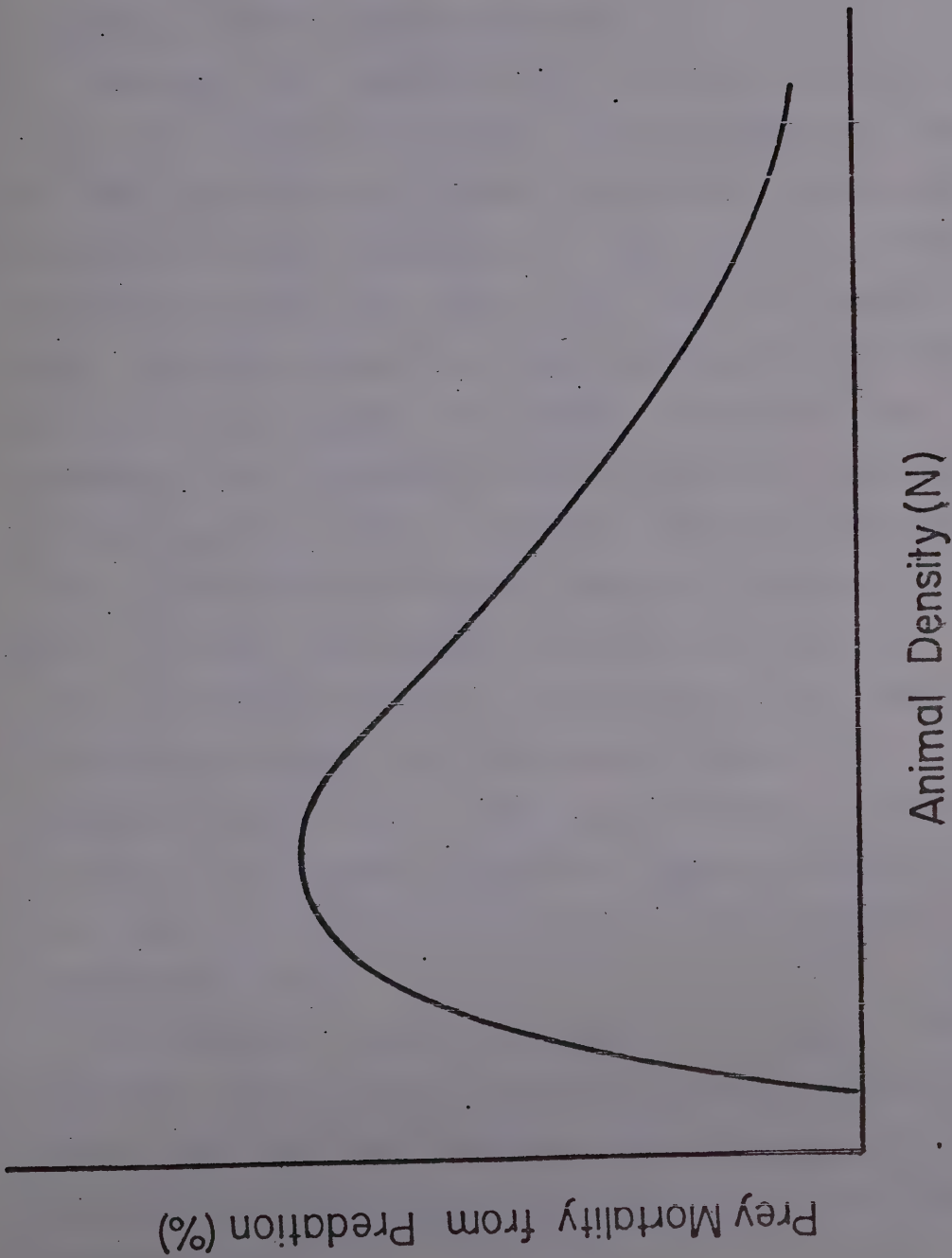
Figure 4. Combined functional and numerical response curve of a typical predator after Holling (1950).

tives. All populations can withstand some additional mortality and there is a limit to the amount of additional mortality any population can tolerate (Connelly 1978). We assumed that competition, predation and hunting are largely (but not completely) additive (noncompensatory).

Combining the competition and predation mortality curves results in a complex (sinusoidal) curve (Holling 1973, Haber et al. 1976, Haber and Walters 1980). If predation is high enough to regulate the prey population, it can push the percent net reproduction curve below zero (Fig. 5b). This produces two stable equilibria; one at low density determined by predation (Kl) and one at high density determined by competition (Ku). Each equilibrium has a surrounding domain of stability separated by an unstable equilibrium (Kc). When prey density is disturbed from either stable equilibrium it will return to it unless it is forced past the unstable equilibrium. The system then flips into another domain of stability and moves to the appropriate new equilibrium. The range of densities where recruitment is negative (Kl to Kc) is termed the "predator pit". The prey population can escape from this situation of negative recruitment (increase above Kc) only if prey numbers are suddenly increased (eg., by immigration) or if predation is reduced.

If predation is not high enough to regulate the prey population then the effect on the net reproduction curve is less dramatic and the prey population will have only one stable equilibrium point although it may be lower than in the absence of predation (Fig. 5a).
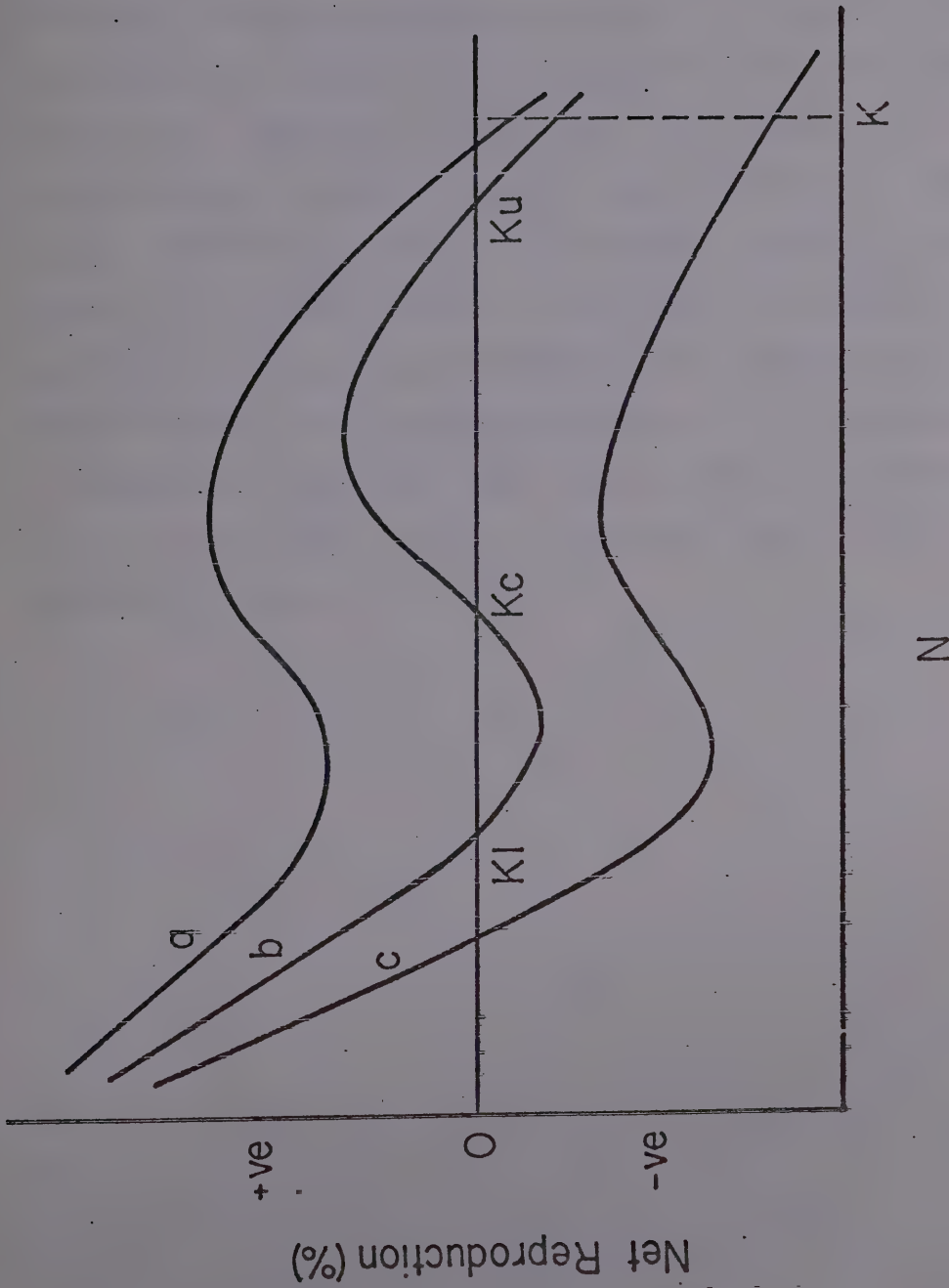
Figure 5. Percent net reproduction curve when logistic population growth (Fig. 3) is combining with a) low, b) moderate and c) high predation mortality (Fig. 4). Kl is a stable low density equilibrium point, Ku is a stable high density equilibrium point, Kc is an unstable equilibrium point, K represents maximum prey density in the absence of predation (c.f. Figure 3).

Alternatively predation may be high enough to prevent caribou numbers from ever escaping its regulatory effect (Fig. 5c).

When hunting mortality is added to the effects of competition and predation the shape of the net reproduction curve stays basically the same but shifts downward. If predation was already high enough to regulate the prey population (Fig. 5b) then hunting pushes the unstable equilibrium point closer to the upper equilbrium and further from the lower equilibrium requiring a larger reduction in predation (more wolves removed or removal to occur over a longer period) to allow the prey to escape from the predator pit (Fig. 6) or precluding any possibility of escape whatsoever (Fig. 6, high hunting pressure). If predation was not regulating the population (Fig. 5a) the addition of hunting would make it more likely to do so, producing any of the situations depicted in Figure 6.
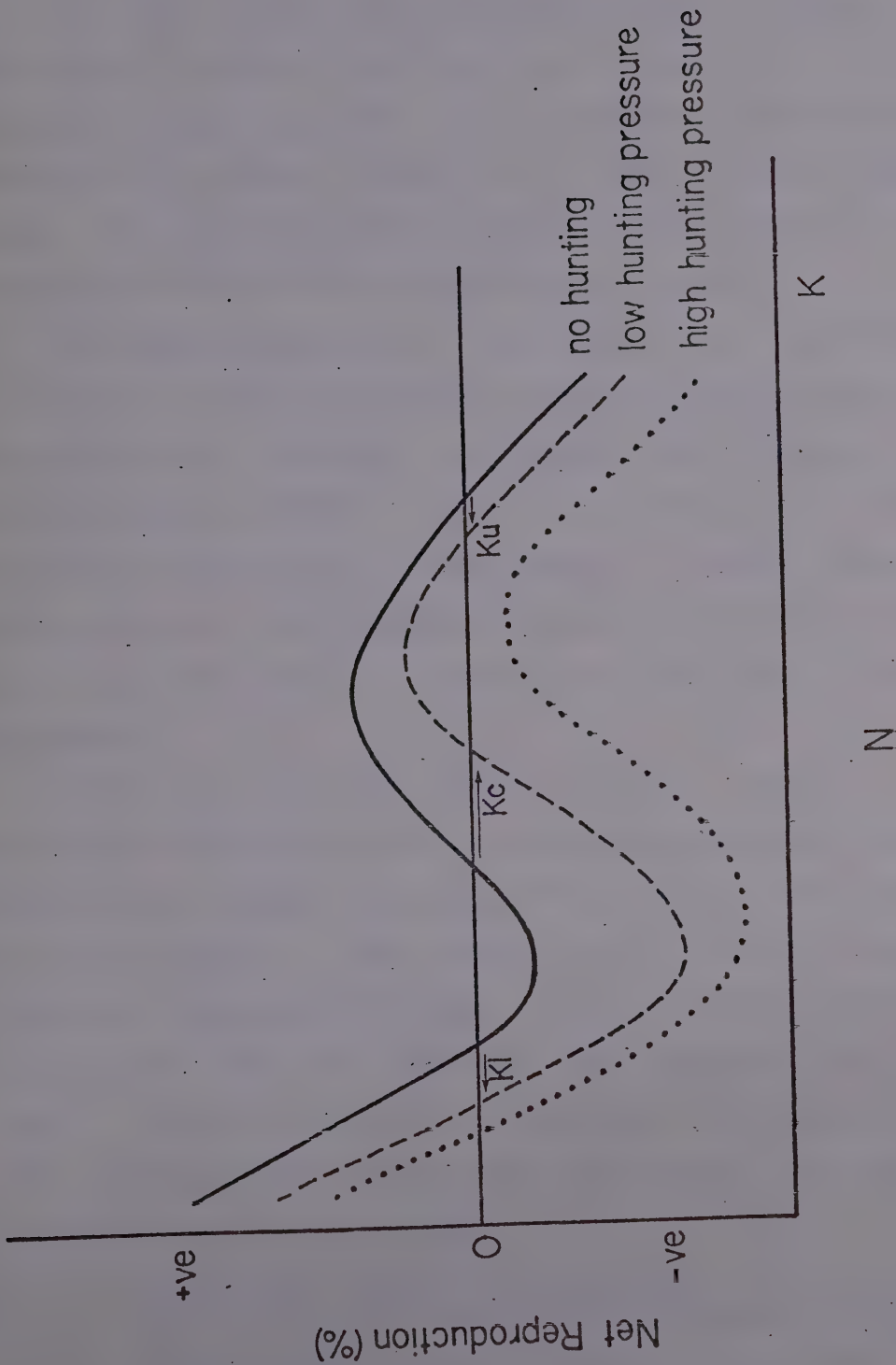
Figure 6. Percent net reproduction curve when logistic population growth is combined with moderate predation (Fig. 5b) and high and low hunting pressure. As hunting pressure increases the lower and upper equilibrium points (Kl and Ku) occur at lower densities and Kc increases.

CASE HISTORIES

Few field studies clearly demonstrate the regulating effect of wolves on prey or the effect of a reduction in the wolf population on prey population size. Nonetheless, many researchers have come to definite conclusions on those subjects (Connelly 1978). The case histories reviewed here are the only wolf removal experiments that led to unambiguous interpretations.

As suggested by predator – prey theory, wolf removal has led to increases in the population size of some ungulate prey species but not others. Moreover, wolf removal led to increased moose (Alces alces) survival in one area but not in another. Fortunately, the effects of wolf removal on caribou numbers are more consistent. All adequately monitored wolf removal programs have been followed by increases in the size of caribou populations.

Gasaway et al. (1981) demonstrated the effects of wolf population reductions on moose, sheep (Ovis dalli) and caribou in Alaska during a 3-year experiment. They radio-collared cow moose in a wolf removal (experimental) area and in a number of nonremoval (unmanipulated) areas. Wolves were killed by shooting from aircraft and wolf densities were determined from aerial counts. During the first year of shooting, wolves were reduced 60%. They were maintained at that level for 2 more years. The results of that experiment were:

1. Moose calf survival increased from 20 to 55% where wolves were removed but not in the nonremoval areas.

2. Moose cow-calf ratios increased 2 to 3 times in the removal area.

3. Adult moose survival improved from 80%/yr to 94%/yr in the removal area.

4.. Data on moose numbers were inadequate to determine if the above effects were translated into a larger population.

5. There was no improvement of lamb survival with wolf removal.

6. In the Delta caribou herd, calf survival to early winter increased from 16% to 48% on the removal area but not in nonremoval areas (see also Davis and Preston 1980).

Ballard and Spraker (1979) worked in an area of Alaska south of Gasaway's study area and found that removing 58% of the wolves had no effect on moose calf survival. In that area grizzly bears (Ursus arctos), not wolves, were killing most of the moose calves.

The three best documented examples of the effect of wolf reductions on caribou numbers comes from the Nelchina, Fortymile and Delta herds in Alaska. During the removal of more than 200 wolves on the Nelchina caribou herd's range between 1948 and 1953 calf survival increased and the population increased. Calf survival declined as wolf numbers later increased on the Nelchina range. In 1966 many wolves were removed and the next year, calf survival again improved (Bergerud 1980).

In the Fortymile herd there was an inverse relationship between caribou and wolf numbers from 1947 to 1959 (Davis et al. 1978). Specifically, low wolf numbers in the late 1940's and early 1950's led to increased calf survival. Wolf numbers increased from 1954 to 1956 and calf survival and caribou numbers declined. Low wolf numbers in 1957 and 1958 led to immediate calf survival increases. Wolf numbers again increased in the 1960's and the caribou populations began a continuous decline.

In relating those data to the theoretical model it appears that; 1) wolves can regulate caribou numbers, 2) caribou densities are about $0.5/km^2$ at equilibrium (Fig. 7), 3) caribou populations do not escape wolf predation (Fig. 5c), and 4) intraspecific competition for food on those ranges studied, does not occur until at least 4 caribou/km^2 (Fig. 7). One complicating factor is that as caribou populations grow densities tend to remain constant because more range is used (Calef 1979, Simmons et al. 1979). We believe that caribou populations can be regulated at any population size to an equilibrium density of $0.5/km^2$.

Bergerud (1978a, 1978b, 1980) has reviewed all the data on caribou demography (i.e. not just wolf removal experiments) and related theory. He found that on average, calf survival increased when wolf numbers were reduced. The rate of caribou population growth was inversely correlated with wolf abundance when the effect of hunting was accounted for.

There is little published disagreement with Bergerud's conclusions. Haber and Walters (1980) conclude that the equilibrium values are different than those specified by Bergerud. They suggest that 3 equilibria exist (Fig. 5) and that 0.4 caribou per km^2 (1 caribou per mi^2) is the unstable density, Kc. However, if this were so, one would not expect to find most caribou populations existing at about that density (Calef 1979).

No other formal hypotheses of population regulation in caribou have been proposed. Kelsall and Klein (1979) think that Bergerud's hypothesis is too simple and emphasize the importance of random events, range conditions (see also Klein 1982), and
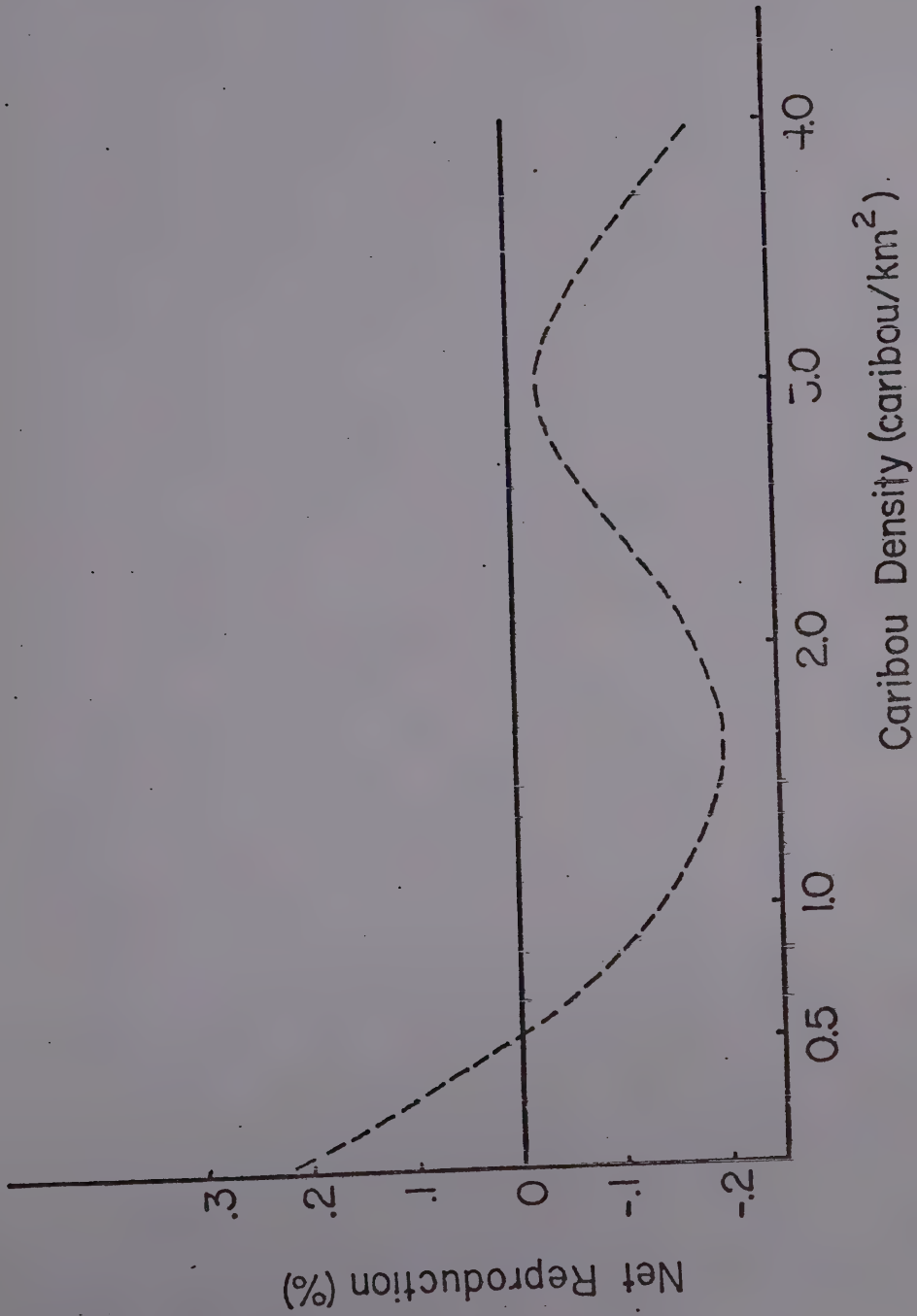
Figure 7. Percent net reproduction curve assumed to represent North American caribou populations experiencing wolf predation. Caribou have only one equilibrium point at about 0.5/km².

disturbance by man in caribou demography. There are no data that suggest to us that those factors can regulate barren-ground caribou populations subject to wolf predation.

CARIBOU AND WOLVES IN THE NWT

In the 1950's intensive wolf poisoning occurred on all NWT barren-ground caribou winter ranges east of Great Bear Lake (Kelsall 1968, Heard 1982). Each year between 1955/56 and 1960/61, the poisoning program killed about 1,800 wolves. The effect on caribou numbers was never monitored and the effect on calf recruitment was poorly documented (no methods recorded, small sample size and results averaged over all areas). The decline; 1) in the number of wolves killed per year, 2) the kill per dollar spent, and 3) the increase in the proportion of pups in the population, suggest that poisoning reduced wolf numbers between 1955 and 1960 (Kelsall 1968). The available data on caribou recruitment (Kelsall 1968) do not show any clear association with relative wolf poisoning efforts (Fig. 8). However, those recruitment data were based on small sample sizes from unknown locations and do not demonstrate that recruitment did not increase in response to wolf reductions.

The NWT data are therefore inadequate to demonstrate the effect of a reduction in the wolf population on caribou populations. The simplest assumption is that the NWT caribou-wolf ecosystem will behave as it does in Alaska. NWT caribou herds exist at about 0.5/km^2 (Calef 1979) as in Alaska but, unlike Alaska, NWT wolves on barren-ground caribou ranges have few alternate big game prey (eg., moose, sheep and muskox [Ovibos moschatus]) available to them. The lack of alternative prey should reduce the possibility of a "predator pit" which is essentially a situation where predator numbers are maintained on alternate prey.
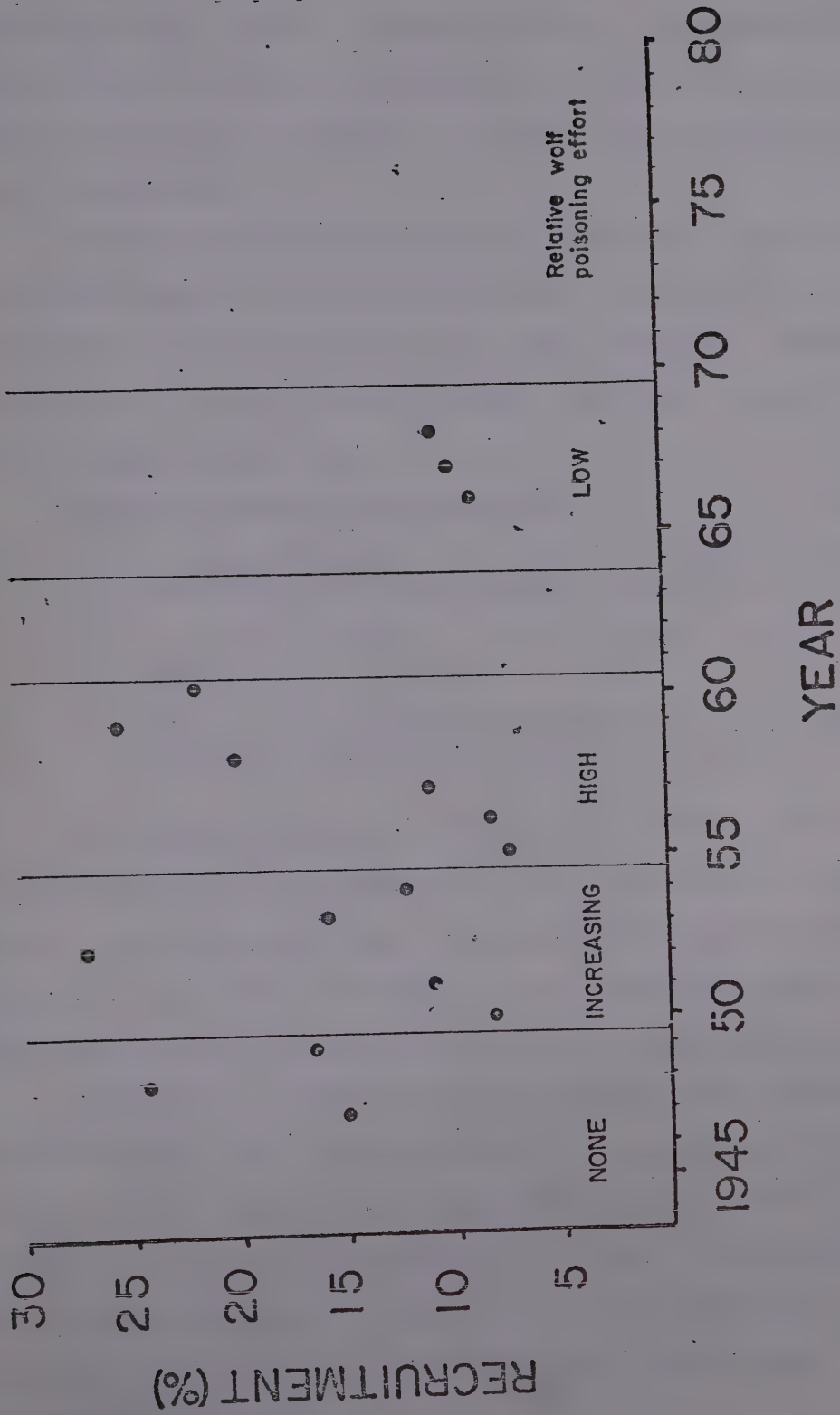
Figure 8. Relationship between recruitment and relative wolf poisoning effort in the N.W.T.

We believe therefore, that a reduction in the NWT wolf population will have a similar effect as in Alaska; increased recruitment. If such an experiment were undertaken in the NWT the effects should be monitored so that we learn as much as possible from the exercise.

We learned almost nothing about the effects of the NWT wolf poisoning program in the 1950's because the predicted effect, an increased caribou population, was never measured. Thirty years later we are facing the same problem and have only the Alaskan data to make predictions.

A proper experiment would include:

1. An accurate measure of changes in caribou numbers or preferably both caribou numbers and calf survival rates.

2. An accurate measure of the relative change of wolf numbers.

3. Measures of the above variables in an unmanipulated population for comparison with the experimental area(s).

An effective program of reducing wolf numbers and increasing calf survival may not result in an increase in caribou population sizes. We would expect only that the caribou population's rate of increase (r) would increase. In a declining population a reduction in wolf numbers may only slow the rate of decline.

Assuming the objective of an increased effort to kill wolves is to maximize r for caribou, without exterminating wolves, until caribou herds increase to predetermined sizes, three questions remain; 1) how many wolves should be killed?, 2) how long should the program last?, and 3) what are the best methods of reducing the wolf populations (including the time of year and the geographical area)?

1. Ecological principles of exploitation are that the maximum sustained yield occurs at a level below that of an unexploited population. Kills of less than the maximum sustained yield also reduce populations below unexploited (natural) levels but not to the levels occurring when the maximum sustained yield is being removed (Krebs 1978: 345). Mech (1970) suggested that wolves can compensate for annual losses by man, of about 50%. Thus 50% is the maximum sustained yield of a wolf population. This does not mean that a wolf population will not be reduced if less than 50% of the population is killed each year.

    If wolves are regulating NWT caribou numbers, then there would be some positive effect on caribou numbers even if less than 50% of the wolf population was removed. The magnitude of the effect on caribou numbers would increase with the number of wolves killed. We feel that it would be almost impossible to exterminate wolves and that there is little risk of removing too few wolves. Killing only a few wolves may not measurably reduce wolf numbers, but it would probably not stimulate wolf reproduction through social disruption in the existing population, because wolves are already hunted. In fact, recent hunting levels (since 1978) may already have reduced wolf numbers, especially on the Bathurst herd range in 1978/79 when Coppermine hunters shot over 1000 wolves.

2.   If the resulting rate of increase for caribou does not increase after an adequate testing period (eg., 3 or 4 years) the program should be terminated. If r increases but remains negative then additional measures must be implemented (eg., caribou hunting restrictions). If r becomes positive, wolves should continue to be killed until the caribou population reaches a predetermined size.   As soon as wolf populations are allowed to increase to natural levels, caribou population growth would be expected to slow dramatically and caribou numbers should continue to be monitored.

3.   Efficient methods of increasing the wolf kill are; 1) poisoning in winter and at occupied dens, 2) aerial shooting in winter, during caribou spring migration and on the caribou calving grounds, and 3) bounties or trapper incentives.   The methods of killing wolves (poisoning, shooting, snaring, etc.) are irrelevant in terms of the effect on caribou numbers.   However, the methods are important in terms of public attitudes, cost efficiency and the ease of monitoring the experiment through data collection.

Poisoning and aerial shooting permit collection of important information such as an index of wolf population size, reproductive rates and age and sex ratios.   Poisoning would cost less than aerial shooting per wolf killed but poisoning is potentially

dangerous to the public, requires the killing of animals for bait and even though poisoning can be remarkably selective in killing wolves, some foxes, ravens, and wolverines would also die (about 1 non-wolf death for every 3 wolves killed, Kelsall 1968). Bounties have generally been discounted as being ineffective at reducing wolf population size (Mech 1970) but if bounties are high enough they could be effective since the recent increase in the average pelt value has resulted in a dramatic increase in the number of wolves killed by hunters (Heard 1982). The greatest effect on caribou's rate of increase should result if all methods were used.

The existing NWT Wildlife Service inventory procedures of population size, trend, and calf survival (Heard and Decker 1980, Heard 1980) can be used as control data if methods remained the same throughout any wolf removal experiments. Changes in wolf numbers could be most easily monitored by the kill per unit effort. Aerial surveys to determine wolf abundance may be useful on the calving grounds but are unreliable in forested areas. Changes in the number of caribou and wolves shot by hunters could greatly influence the results of any experiment and therefore must be measured. Data on population structure and reproductive rates of both caribou and wolves would help monitor any experiment but they are not vital.

We have purposely avoided using the phrase "wolf control" in this paper because it means different things to different people. "Wolf control" can mean either; 1) a reduction in wolf population size (eg., Kelsall 1968: 258), or 2) an increased effort to kill wolves -- usually through a bounty system, poisoning or aerial

shooting (eg., Mech 1970). The problem with the second definition is that not all "control" efforts are successful at reducing wolf population size (eg., bounties, Mech 1970: 346). The problem with the first definition is that "control" means different degrees of population reduction to different writers. "Control" may mean; a) any amount of reduction in the wolf population (eg., Kelsall 1968: 258). "It appeared that (wolf) control was being achieved and that the population was declining." Alternatively, "control" may mean a reduction in wolf numbers below the maximum sustainable yield (eg., Mech 1970: 64). "Further, in order to control wolf numbers, then, it appears that at least 50% of the animals of this age (5 to 10 months or older) must be killed each year."

CONCLUSIONS

We predict that an increased effort to kill wolves would benefit NWT caribou herds. Caribou populations may grow or decline at a slower rate depending on hunting pressure and the amount of the decline in wolf population.

ACKNOWLEGEMENTS

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